REVISION OF THE LUMBRICULID OLIGOCHAETE ECLIPIDRILUS EISEN, 1881, WITH DESCRIPTIONS OF THREE SUBGENERA AND ECLIPIDRILUS (LEPTODRILUS) FONTANUS N. SUBG., N. SP. FROM PENNSYLVANIA

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Abstract.—A division of seven species of Eclipidrilus into the three subgenera Eclipidrilus, Premnodrilus, and Leptodrilus is based on characteristics of the reproductive systems. Eclipidrilus fontanus n. sp. is similar to E. lacustris (Verrill, 1871), but has paired reproductive structures. A key to species of Eclipidrilus and records of recent collections are included

Microdrile oligochaetes of the genus *Eclipidrilus* have a holarctic freshwater distribution. Six species occur in North America, one of which is also known from the British Isles, and a single species is restricted to Asiatic U.S.S.R. In the United States *Eclipidrilus* species are found in the Great Lakes and Mississippi River drainages, in waters of both the Rocky and Appalachian mountains, and in streams of the southeastern states. They have been found in both river and lake habitats and some species are restricted to unpolluted locations. Specimens are rare, in some places locally abundant, and current information suggests a restricted distribution. An accurate generic diagnosis has not appeared in the literature since the discovery of *E. levanidovi* Sokolskaya, 1977, which has reproductive structures more anterior than other species. For an historical review of the literature pertaining to this genus see Wassell (1981). A revised diagnosis is provided here.

Eclipidrilus Eisen, 1881

Diagnosis.—Prostomium prolobous, rounded or produced into proboscis-like extension. Preclitellar segments biannulate. Setae simple pointed with nodulus distal, similar throughout. Two pairs of posterior lateral blood vessels present. Male pores paired on VIII or X; or single median on X. Ovarian pores paired on IX or XI. Spermathecal pores paired on VII or IX; one or two median on IX; single median on VIII and IX. Testes: one pair in VIII or X; two pairs in IX and X; always present in segment bearing male pores. Vasa deferentia one or two pairs. Atria: tubular, with thick muscular walls of spirally arranged fibers; an outer layer of longitudinal fibers may be present. Prostatic cells surrounding the atria may be compact or sparse. Penes paired or single, of three general types: small protrusible; long muscular eversible; retractile with thin cuticularized sheaths. Ovaries: one pair in IX or XI, always present in segment immediately posterior male pores. Spermathecae: paired in VII or IX; one or two median in IX; one in both VIII and IX; always present in segment immediately anterior male pores.

Type-species. - Eclipidrilus frigidus Eisen, 1881, by original designation.

Eclipidrilus (Eclipidrilus) Eisen, 1881

Diagnosis.—Eclipidrilus with long muscular eversible penis. Penis without cuticular sheath and contained in muscle layer. Atrium with wide lumen posteriorly. Atrium constricted anteriorly with narrow lumen, before widening to contain penis. Penis formed from tissue lining anterior inside of atrium, which is continuous with atrium posteriorly and with longitudinal body wall muscle anteriorly. Penial structure not attached to dorsal body wall by retractor muscles. Atrium and male structures paired or single.

Type-species. - Eclipidrilus frigidus Eisen, 1881.

Remarks.—This is the nominate subgenus which in addition to E. (E.) frigidus Eisen, 1881, includes E. (E.) asymmetricus (Smith, 1896). The latter species was originally described as Mesopodrilus due to its singular penis and atrium. Because of the morphological similarity of the reproductive structures these two species are included in this subgenus.

In addition to its unpaired atria, *E.* (*E.*) asymmetricus has a prostomial extension. This species has not been collected since its original description. A recent attempt by the author to obtain it from samples taken at the type-locality (Quiver Lake, Illinois) was unsuccessful. Paratype material examined (NMNH 24588) is a post-reproductive specimen.

Eclipidrilus (E.) frigidus has paired reproductive structures and a blunt prostomium. Lectotype material was examined (NMNH 25565, 32911). This species has been recently collected from the Salmon River, Veil Falls, Idaho in 1976 by R. L. Denton. I am grateful to the collector and D. R. Spencer for these specimens, which are placed in the museum of the Louisiana State University (LSU 3176).

Eclipidrilus (Premnodrilus) Smith, 1900, new rank

Diagnosis. — Eclipidrilus with long retractile penis with cuticularized sheath and contained in muscle layer. Atrium with wide lumen posteriorly, constricted anteriorly to form duct attached to penis. Penis surrounded by muscle layer anteriorly continuous with longitudinal body wall muscle and may be attached to dorsal body wall posteriorly by retractor muscles. Atria and male structures paired.

Type-species. - Premnodrilus palustris Smith, 1900.

Remarks.—The subgenus (Premnodrilus) is designated for the generic name chosen by Smith in 1900 for species which possess a reproductive system of this type. An important characteristic of this subgenus is the thin cuticularized penis sheath, which has been described previously only by Sokolskaya (1977). Three species in this subgenus are distinguished by segmental location of reproductive structures, by condition of the prostomium, and dimensions of the atria. This subgenus includes: E. (P.) palustris (Smith, 1900), E. (P.) daneus Cook, 1966, and E. (P.) levanidovi Sokolskaya, 1977.

Eclipidrilus (P.) daneus has a prostomial extension and the atria have comparatively thin walls so that the lumen comprises about two-thirds of the diameter of the atria. This species has been collected from seven Louisiana parishes during 1979–1981; specimens are in the museum of the Louisiana State University (LSU 3178–3186). The holotype and paratypes have been examined (NMNH 32907, 32908).

Eclipidrilus (P.) palustris has a prostomial extension and atria have thicker walls than E. (P.) daneus so that the lumen comprises about one-third of the atrial diameter. This species has recently been collected from three counties in Florida (LSU 1490, 1949, 2156). A study of sagittal sections of one of these specimens reveals a glandular material in X, similar to that described for Spelaedrilus multiporus Cook, 1975, and a slight elaboration of the spermathecal duct, similar to that in E. (E.) frigidus, but less extensive. An additional pair of testes in IX was observed in this specimen. The cotype (NMNH 25509) was examined.

Eclipidrilus (P.) levanidovi is placed in this subgenus because of the cuticular penis sheath evident in the description. The reproductive structures are displaced anteriorly by two segments in contrast to all other Eclipidrilus species. No specimens were available for examination. The original description is in Russian.

Eclipidrilus (Leptodrilus), new subgenus

Diagnosis.—Eclipidrilus with short protrusible penis without cuticularization and not contained in muscle layer. Atrium with wide lumen posteriorly, constricted anteriorly to become the penis. Penis formed from papilla structure of body wall muscles, no retractor muscles attached dorsally. Atrium and male structures paired or single.

Type-species. - Lumbricus lacustris Verrill. 1871.

Remarks.—This new name is derived from the Greek "leptos" meaning slender, thin, small and weak. This refers to the small thin penis with weak musculature. The two species in this subgenus differ in the paired or unpaired condition of the reproductive systems. The unifying characteristic of this subgenus is the morphology of the atria and penes. This subgenus includes: E. (L.) lacustris (Verrill, 1871), and E. (L.) fontanus, new species.

Eclipidrilus (L.) lacustris has a single median atrium. It is reported from Lake Superior, where the type-collection was made, and recently from Cayuga Lake, New York (Spencer 1978) and Quebec, Canada (Cook in Brinkhurst and Cook, 1966). The Cayuga Lake specimen was made available to me for study and is placed in the museum of the Louisiana State University (LSU 3177). Lectotype and paralectotype specimens were examined (NMNH 15587, 17947, 32667).

Eclipidrilus (Leptodrilus) fontanus, new species Figs. 1, 2

Material examined. — HOLOTYPE: NMNH 068641, Pennsylvania: Somerset County, Forbes State Forest, Wild Cat Spring, 22 Jul 1978, 1 whole mount specimen. PARATYPES: NMNH 068642, same locality and date, 10 whole specimens in formalin. NMNH 068643, same locality and date, 7 whole mount specimens. NMNH 068644, same locality and date, 1 specimen, 7 slides, transverse sections 20 μm thick. NMNH 068645, same locality, 29 May 1979, 1 specimen, 4 slides sagittal sections and 1 slide whole mount of posterior end. NMNH 068646, same locality, 29 May 1979, 1 specimen, 3 slides sagittal sections and 1 slide whole mount of posterior end. LSU 3053, same locality, 22 Jul 1978, 9 whole mount specimens and 1 sagittal sectioned specimen. ADDITIONAL SPECIMENS (all from Pennsylvania): LSU 3188, same locality, 22 Jul 1978, 1 transverse sectioned specimen. LSU 3046, same locality, 23 Oct 1976, 4 whole specimens. LSU 3047,

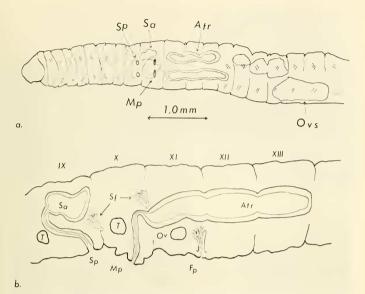


Fig. 1. Eclipidrilus fontanus: a, Holotype, drawing of whole mount from prostomium to XX; b, Diagram from sagittal sections of IX-XIII. Atr = atrium, Mp = male pore, Ovs = ovisacs, Sa = spermathecal ampulla, <math>Sp = spermathecal pore, Fp = female pore, Ov = ovary, Sf = sperm funnel, t = testes.

same locality, 28 May 1978, 1 whole specimen. LSU 3048, Somerset County, Tub Mill Run, Forbes State Forest, 22 Jul 1978, 5 whole specimens. LSU 3049, Fayette County, Bear Run, 24 Sep 1976, 5 whole specimens, coll. Dr. W. P. Coffman. LSU 3050, same information, 9 Sep 1976, 5 whole specimens. LSU 3051, Fayette County, Dunbar Creek near Dunbar, Limestone Run at Game Commission Road, 23 Feb 1975, coll. J. Duncan, 2 whole specimens. LSU 3052, Somerset County, Powdermill Creek, Youghiogheny drainage, 28 Jan 1975, coll. Dr. J. Sykora, 2 whole specimens. (All specimens collected by author unless otherwise noted.)

Etymology.—From the Latin adjective "fontanus" relating to spring. This refers to the type-locality.

Diagnosis. -64 to 108 segments. Length up to 31 mm, preserved; diameter 0.6 mm at II, 0.8 mm at X. Prostomium rounded, as long as wide at peristomial junction. II–VIII with secondary annulations. Setae 93–253 μ m long, ratio of point to node setal length to total setal length 0.28–0.30.

Testes paired, present in X, present or absent in IX. Two pairs male funnels present anterior septa 9/10 and 10/11. Atria paired, 0.3–1.4 mm long, cylindrical,

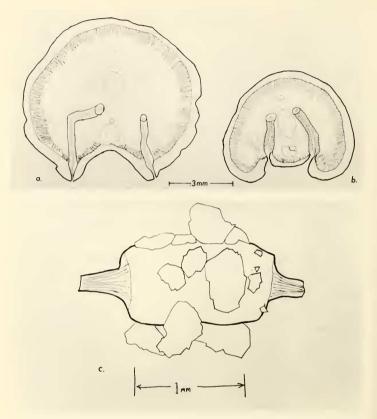


Fig. 2. Eclipidrilus fontanus: A, Transverse section of X through penial ducts and penis; B, Transverse section through spermathecal pores and ducts; C, cocoon with sand grains attached.

may extend to XIII, consisting of spiral muscles ca. 45 μ m thick, diameter range 132–379 μ m. Ratio of diameter of lumen to external diameter of atrium 0.60–0.75. Penes paired on X, protrusible extensions of distal duct of atrium without cuticularization.

Ovaries paired in XI, ovarian funnels open anterior 11/12. Spermathecae paired in IX, may extend into X, ampulla pear-shaped to ovoid, ca. 275 μ m long, 200 μ m wide. Spermathecal ducts distinct with uniform diameter ca. 25 μ m, no muscular thickening of the duct, ca. 300 μ m long, open on IX.

Table 1.-Comparison of species characteristics in Eclipidrilus.

Species	Penes	Atrium (diameter)	% lumen	Testes; funnels	Spermathecae	Ovaries	Prostomial extension
E. asymmetricus	Long eversible	Single	80	X; 10/11	IX, paired	IX	Present
E. frigidus	Long eversible	Paired (170–200 μm)	80	IX, X; 9/10, 10/11	IX, paired	IX	Absent
E. daneus	Long cuticularized retractile	Paired (120–220 μm)	80	X; 9/10, 10/11	IX, paired	X	Present
E. levanidovi	Long cuticularized retractile	Paired (177–190 μm)	70	VIII; 8/9	VII, paired	×	Absent
E. palustris	Long cuticularized retractile	Paired (270–300 μm)	30	(IX), X; 9/10, 10/11	IX, paired	īx	Present
E. lacustris	Small protrusible	Single (200–300 μm)	80	IX, X; 9/10, 10/11	IX, single or paired; VIII and IX, single	×	Absent
E. fontanus n. sp.	Small protrusible	Paired (130–380 μm)	80	(IX), X; 9/10, 10/11	IX, paired	IX	Absent

Remarks.—This new species resembles E. (L.) lacustris except for the paired arrangement of reproductive structures. Two pairs of vasa deferentia occur in this species and one pair of testes is always present in X. A second pair of testes has been observed in IX in some specimens. The presence of anterior testes is probably not as strong a taxonomic character as previously thought. The occurrence of testicular tissue in IX in this species is indicative of an early maturity state and loss of gonad material in IX may result from sexual activity.

This species has been collected only from very clean, cold mountain streams. The type-locality is a cold, sandy bottom bubbling spring. The cocoon is barrel-

shaped with sand grains attached.

Discussion.—This study reinforces the genus Eclipidrilus as a valid taxon. All species of Eclipidrilus are united because of the spiral arrangement of muscle fibers which comprise the atrium. The loss of bilateral symmetry in the reproductive system is an advanced condition in this genus and has occurred in two species. (Table 1). It has been suggested (Holmquist 1976) that the occurrence of unpaired reproductive organs is so unique within the Lumbriculidae (except Tatriella Hrabě, 1936) that the two species of Eclipidrilus with unpaired systems are deserving of generic rank. These species were originally in Mesopodrilus Smith, 1896, which was made a junior synonym of Eclipidrilus by Hrabě (1936) after Michaelsen (1901). The discovery of E. (L.) fontanus (with paired reproductive structures), which is similar to the unilateral E. (L.) lacustris, provides evidence that the bilateral arrangement is ancestral. Consequently, undesirable polyphyletic taxa would result from the elevation of these two species to a genus separated from Eclipidrilus.

Key to species of Eclipidrilus

1.	Single atrium
_	Atria paired
2.	Atrium with constriction. Penis muscular, elongate. Spermathecae paired with pores median. Prostomial extension present. Illinois (unreported since 1896) E. (E.) asymmetricus (Smith, 1896)
-	Atrium not constricted. Penis simple. Single spermatheca with median pore. Prostomium rounded. Cayuga Lake, New York; Lake Superior; Quebec, Canada; British Isles
	E. (L.) lacustris (Verrill in Smith and Verrill, 1871)
3.	Male pores on VIII. Spermathecae open on VII. U.S.S.R., Chukotski
	Peninsula E. (P.) levanidovi Sokolskaya, 1977
-	Male pores on X. Spermathecal pores on IX
4.	Penes with lightly cuticularized sheaths. Prostomial extension
	present 5
_	Penes without cuticularized sheaths. Prostomium rounded 6
5.	Atrial muscle 60–100 µm thick, lumen comprises ca. one-third of atrial
	diameter. Florida, South Carolina E. (P.) palustris (Smith, 1900)
_	Atrial muscle 6-20 µm thick, lumen comprises ca. two-thirds of atrial
	diameter. Louisiana, Montana, South Carolina
	E. (P.) daneus Cook in Brinkhurst and Cook, 1966
6.	Atria constricted, extending to XV. Penes muscular, elongate. Spermathe-
	cal ducts elaborate. California, Idaho E. (E.) frigidus Eisen, 1881

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